

# NESTOTUS AND TOIYABEA, TWO NEW GENERA OF ASTERACEAE: ASTEREAEE FROM THE WESTERN UNITED STATES AND CANADA

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## ABSTRACT

*Nestotus* is described as a new ditypic genus from the western United States and the Yukon Territory, Canada, to accommodate *Stenotus macleanii* (Brandege) A. Heller and *Stenotus stenophyllus* (A. Gray) Greene, resulting in two new combinations *N. macleanii* and *N. stenophyllus*. Sequence-based phylogenetic investigations consistently demonstrate and robustly support the relatedness of these two taxa and their distinctiveness from the type species, *S. acaulis* (Nutt.) Nutt., and other taxa placed in *Stenotus*. *Toiyabea* is described as a monotypic genus from Nevada to accommodate *Tonestus alpinus* (L.C. Anderson & S. Goodrich) G.L. Nesom & D.R. Morgan, resulting in the new combination *Toiyabea alpina*. This species, *Petradoria*, plus *S. acaulis* and *S. armerioides* Nutt. constitute a well-supported polytomy sister to *Solidago* and related taxa in our molecular-based phylogeny.

## RESUMEN

Se describe *Nestotus* como un género ditypico nuevo del oeste de los Estados Unidos y del territorio de Yukón en Canadá para ubicar a *Stenotus macleanii* (Brandege) A. Heller y a *Stenotus stenophyllus* (A. Gray) Greene con las consecuentes combinaciones nuevas *N. macleanii* y *N. stenophyllus*. La relación entre estas dos especies y las diferencias entre ellas, y la especie tipo, *S. acaulis* (Nutt.) Nutt., y otras especies de *Stenotus* es demostrada consistentemente con un alto apoyo en las investigaciones basadas en secuencias de ADN. Adicionalmente se describe *Toiyabea* como un género monotípico de Nevada para ubicar a *Tonestus alpinus* (L.C. Anderson & S. Goodrich) G.L. Nesom & D.R. Morgan con la consecuente nueva combinación *Toiyabea alpina*. Esta especie, *Petradoria*, junto con *S. acaulis* y *S. armerioides* Nutt. constituyen en nuestra filogenia molecular una politomía con alto apoyo, la cual es hermana de *Solidago* y los táxones emparentados.

## INTRODUCTION

The sequence-based investigations of Roberts (2002) and Roberts and Urbatsch (2004) focused on sorting out relationships among several genera of the tribe Astereae. The patterns of relationship unveiled by the sequence-based investigations are in many cases incongruent with those inferred from morphology. Among the taxa included in those investigations were the six species of *Stenotus*

Nutt. and the eight known species of *Tonestus* A. Nelson. Those investigations (Roberts 2002; Roberts & Urbatsch 2004) revealed that *Stenotus* as defined by Morse (1998) and *Tonestus* as defined by Nesom and Morgan (1990) are not monophyletic. A single species, *S. armerioides*, clustered with *S. acaulis*, the type of the genus (Fig. 1), while the other species of *Stenotus* either were more closely aligned with other genera rather than with their congeners or their relationships were not fully resolved. Species of *Tonestus* included in the sequence-based investigations were also not closely aligned with each other. Three species including the type, *T. lyallii* (A. Gray) A. Nelson, were part of a grade under the *Chrysothamnus/Acamptopappus* lineage, whereas the other five species were associated with other lineages (Fig. 1). Here we address the cladistic relationship of three taxa: *Stenotus macleanii* (Brandege) A. Heller, *S. stenophyllus* (A. Gray) Greene, and *Tonestus alpinus* (L.C. Anderson & S. Goodrich) G.L. Nesom & D.R. Morgan. The specifics of other species previously treated in *Stenotus* and *Tonestus* are addressed elsewhere (Brouilet et al. 2004; Urbatsch et al. 2005) or will be the subject of further investigation. In the sequence-based investigation summarized in Figure 1, *S. macleanii* and *S. stenophyllus* were consistently resolved with robust bootstrap and Bayesian support as sister taxa in all trees, though their relationship to other taxa included in the study was not fully resolved (Roberts 2002; Roberts & Urbatsch 2004). These taxa were also sister in the morphological study of the genus *Stenotus* by Morse (1998). Morse (1998) proposed that these taxa were closely related to *S. lanuginosus* (A. Gray) Greene and indicated that they are united by characteristics that include thin, stipitate-glandular leaves and herbaceous, stipitate-glandular phyllaries of equal lengths in two series. The sequence-based investigations of Roberts (2002) and Roberts and Urbatsch (2004) were inconclusive in reference to this proposition because the relationship of the *S. macleanii* / *S. stenophyllus* clade to *S. lanuginosus* was not fully resolved on all phylograms. Both clades typically were part of a large polytomy (Fig. 1). As a result of the consistent, strong, sequence-based support of *S. macleanii* and *S. stenophyllus* and their morphological distinctness from other *Stenotus* (sensu Morse 1998) and all other taxa included in the molecular investigation, we describe the genus ***Nestotus*** to accommodate these two species.

***Toiyabea*** is proposed to accommodate one species, *Tonestus alpinus*, which was previously placed in *Haplopappus* by Anderson (1980) and subsequently transferred to *Tonestus* by Nesom and Morgan (1990) in their reinstatement of that genus. The proposition of this new genus necessitates the combination *Toiyabea alpina*. In the sequence-based investigations (Roberts 2002; Roberts & Urbatsch 2004), *Tonestus alpinus* was most often placed in a lineage with *Petradoria pumila* (Nutt.) Greene, *Stenotus acaulis*, and *S. armerioides*. The position and relationships among the four taxa in that lineage were not congruent across analytical methods or data sets. Bayesian analysis of the ITS and combined

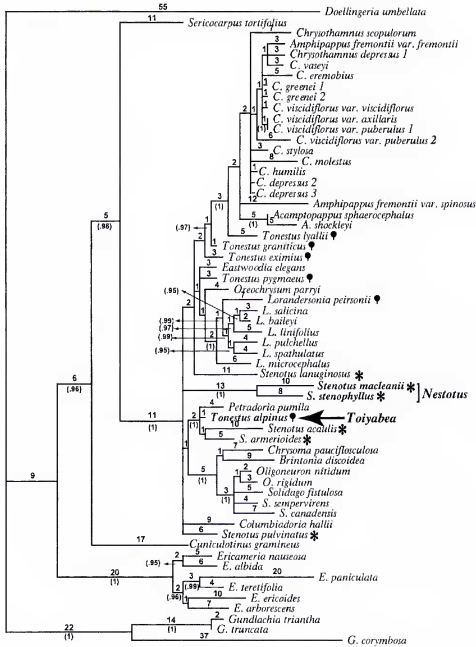


FIG. 1. Fifty percent majority rule consensus tree resulting from Bayesian analysis of combined ETS and ITS data sets is shown. Taxa regarded as *Stenotus* (sensu Morse 1998) are marked with the asterisk “\*”. The symbol indicates species of *Tonestus* (sensu Nesom & Morgan 1990). Not included in the figure but part of our investigations were *T. aberrans* and *T. kingii* which proved to be aligned with subtribe Machaerantherinae (Brouillet et al. 2004). The large arrow indicates taxa treated herein as *Toiyabea*; the bracket marks those considered *Nestotus*. This figure is modified from one published in Roberts and Urbatsch (2004). More details and a discussion of results from this and other analyses based on these sequence data are also given in that publication.

data sets supported a trichotomy composed of *Petradoria*, *Tonestus alpinus*, plus a weakly supported clade consisting of *Stenotus acaulis* and *S. armerioides* as shown in Fig. 1 (Roberts & Urbatsch 2004). In both analyses this lineage was sister to a clade containing *Solidago* and taxa representing three other genera. In the Bayesian analysis of the ETS data, *Petradoria* was sister to the *Solidago* lineage whereas *Tonestus alpinus*, *Stenotus acaulis* and *S. armerioides* were part of a polytomy basal to *Petradoria*. Unlike the previous two situations, analyses employing parsimony and maximum likelihood of the combined ETS/ITS data matrices resulted in phylograms in which the four taxa under consideration formed an unresolved lineage with weak to moderate bootstrap support (Roberts & Urbatsch 2004). This clade was a weakly supported sister to the *Solidago* lineage in the maximum likelihood analysis, but part of a large polytomy above *Sericocarpus* in the parsimony analysis.

The proposed close relationship of *Tonestus alpinus* to *T. eximius* (Anderson 1980) is not supported by the nrDNA data. Instead, this taxon is apparently closely aligned to *Petradoria* and the two species of *Stenotus*. The two species of *Stenotus* are morphologically distinctive from *Petradoria* and merit continued recognition at generic rank. We propose *Toiyabea* to accommodate *Tonestus alpinus* because of its distinctiveness from *Petradoria* and *Stenotus* and its failure to aggregate with any specific taxon in the sequence-based analyses.

#### NOMENCLATURAL TREATMENT

**Nestotus** R.P. Roberts, Urbatsch & Neubig, gen. nov. TYPE: *Haplopappus stenophyllus* A. Gray in Torrey, Wilkes, U.S. Expl. Exped. 17:347. 1874 = *Nestotus stenophyllus* (A. Gray in Torrey) R.P. Roberts, Urbatsch & Neubig, combination made herein. *Stenotus* Nutt., in part, Trans. Amer. Philos. Soc. ser. 2: 7:334. 1840. *Stenotus stenophyllus* (A. Gray in Torrey) Greene, Erythraea 2:72. 1894.

Plantae suffrutices tegetes formantes; caules ad 12 cm plures e caudice lignoso ramoso; folia caulina ut videtur fasciculata marcescentia; pedunculi 1–5 cm, involucri 2-seriati vel raro 3-seriati; Hosculi disci 9–27, rami stylorum lanceolati; pappi setae albidae 30–50.

Mat-forming subshrubs. Stems to 12 cm, several arising from a branching, woody caudex, prostrate to upright, bark becoming dark brown to gray, flaky to fibrous when older; twigs, mostly ascending, whitish tan to purplish, mostly 1–4 cm, generally pubescent and often stipitate glandular. Leaves cauline, crowded, appearing fascicular, ascending to spreading, often marcescent, linear to narrowly spatulate, 3–21 × 0.3–2.0 mm, ± clasping, often whitish basally, glabrous to scabrous or villous, often stipitate-glandular, margins scabrous with short, spreading-ascendant cilia, apices, acute to obtuse, often minutely mucronate, generally 1-nerved. Capitulescences solitary, peduncles 1–5 cm, usually pubescent, often stipitate glandular. Involucres campanulate to hemispherical 5–10. Phyllaries ± imbricate, 2 or rarely 3 seriate, outer linear or narrowly oblong to oblanceolate, inner narrowly oblanceolate, stipitate-glandular abaxially.

chartaceous proximally, herbaceous and pliable distally, sometimes weakly keeled, margins scarious, 1-nerved (rarely weakly 3-nerved). Capitula radiate, florets 20–30. Ray florets 5–11, pistillate, fertile, corollas yellow, laminae elliptical to oblong, 4.5–12 × 1.3–5.5 mm. Disk florets 9–27, bisexual, fertile, corollas narrowly or broadly vase-shaped, 4.5–7.3 mm, lobes 0.8–2 mm, tubes glabrous to pubescent. Style-branches lanceolate, 1.2–2.5 mm, appendages 0.6–1.3 mm. Cypselae, 3.7–5 mm, pubescent. Pappi whitish, ±30–50, setose bristles, to 6.0 mm, same on ray and disk florets.  $x = 9$ .

*Etymology.*—*Nestotus* is an anagram derived from the generic name *Stenotus*, in which the two species in this genus have previously resided.

*Prominent features, distribution, and relationships.*—Phylogenetic studies (Roberts 2002; Roberts & Urbatsch 2003, 2004; Urbatsch et al. 2004) indicate that the two species placed together in this genus deserve taxonomic distinction. They are both mat-forming subshrubs from the northwestern United States and Yukon Territory, Canada, characterized by crowded, linear, prominently uninervate leaves. The two can be distinguished from each other by leaf pubescence features and geographic distribution (Morse 1998). Morse (1998) also indicated a close relationship with *S. lanuginosus*, which is not supported by the nuclear ribosomal data of Roberts and Urbatsch (2004). The relationship of this genus to others investigated is not fully resolved and is in need of further study.

Morse (1998) observed that *Stenotus acaulis* and *S. armerioides* intergrade in regions of sympatry and he suggested this might be due to interspecific hybridization. On the other hand, *S. stenophyllus* (*Nestotus stenophyllus*) and *S. acaulis* do not appear to intergrade or hybridize where they are sympatric. These observations are consistent with the relationships shown by sequence data that support a close relationship between *S. acaulis* and *S. armerioides* and a more distant affinity of these species with *Nestotus* (Fig. 1).

***Nestotus macleanii*** (Brandege) R.P. Roberts, Urbatsch & Neubig, comb. nov.

BASIONYM: *Haplopappus macleanii* Brandege, Bot. Gaz. 27:448. 1899. *Stenotus macleanii* (Brandege) A. Heller, Muhlenbergia 17. 1900. *Stenotopsis macleanii* (Brandege) A. Nelson, Bot. Gaz. 37:261. 1904. TYPE CANADA. YUKON TERRITORY: near Dawson, 1848, J. MacLean s.n. (HOLOTYPE: US, fragment UC).

*Stenotus borealis* Rydb., Bull. N.Y. Bot. Gard. 2:184. 1901. TYPE CANADA. YUKON TERRITORY: foot of Lake Lebarge, 23 Jun 1899, J.B. Tarleton 51 (HOLOTYPE: US, fragment UC).

*Distribution, ecology, and relationships.*—This taxon has been reported only from the Yukon River drainage in southwestern Yukon Territory, Canada (Morse 1998). It inhabits rocky slopes, grasslands, and river bluffs. *Nestotus macleanii* is the more northern of the two species in the genus. It is found at elevations ranging from 450–850 meters and flowers in late spring. The close relationship of *N. macleanii* to *N. stenophyllus* was highlighted by Hall (1928) and Morse (1998) and is confirmed by the sequence-based investigations. The two taxa are

very similar morphologically but can be distinguished by differences in pubescence and geographic distribution, as highlighted in the key to species at the end of this treatment.

**Nestotus stenophyllus** (A. Gray in Torrey) R.P. Roberts, Urbatsch & Neubig, comb. nov. BASIONYM: *Haplopappus stenophyllus* A. Gray in Torrey, Wilkes, U.S. Expl. Exped. 17:347. 1874. *Aster stenophyllus* (A. Gray in Torrey) Kuntze, Revis. Gen. Pl. 1:318. 1891. *Stenotus stenophyllus* (A. Gray in Torrey) Greene, Erythea 2:72. 1894. *Hoorebekia stenophylla* (A. Gray in Torrey) Piper, Contr. U.S. Natl. Herb. 11:561. 1906. TYPE: UNITED STATES. [Washington] "WASHINGTON TERRITORY." [Yakima or Kittitas Co.] Spipen (Naches) River to the north fork of the Columbia River, 1838-1842, Pickering & Brackenridge s.n. (HOLOTYPE: GH)

*Distribution, ecology, and relationships.*—*Nestotus stenophyllus* is found in California, Idaho, Nevada, Oregon, and Washington. It inhabits sagebrush steppe on basaltic, rhyolitic, or granitic soils at elevations of 900-2300 meters. Flowering occurs mid to late spring. Its close relationship to *N. macleanii* has been previously discussed and affinities to other taxa are uncertain at this time.

**Toiyabea** R.P. Roberts, Urbatsch & Neubig, gen. nov. TYPE: *Haplopappus alpinus* L.C. Anderson & S. Goodrich, Great Basin Naturalist 40:73. 1980 = *Toiyabea alpina* (L.C. Anderson & S. Goodrich) R.P. Roberts, Urbatsch & Neubig, combination made herein. *Tonestus alpinus* (L.C. Anderson & S. Goodrich) G.L. Nesom & D.R. Morgan, Phytologia 68:177. 1990.

Herbae perennes et lignosae 0.5-2.0 dm altae; caules valde glandulosi; folia in basi obovata vel oblanceolata serrata vel dentata 3-7 cm longa 10-36 mm lata, folia caulina angustiora et serrata 3-5.5 cm longa 8-18 mm lata; capitula discoidea solitaria vel in cymis; involucria 10-12 mm longa circa 7 mm lata; phyllaria 21-28, exterioribus ovatis et folio similibus et glandulosis, interioribus angustis; flosculi 29-55 flavi, corollis 5.8-7.1 mm longis, lobis circa 1.3 mm longis; cypselae 4-5 mm longae et pubescentiae.

Perennial herbs, short rhizomatous, woody only at base, to 1.0(-2.0) dm tall. Stems several arising from caudex, typically unbranched, green, densely pubescent, hairs stipitate glandular. Leaves basal and cauline; ascending to spreading, both types similar, the latter somewhat reduced distally and sessile, spatulate to obovate or oblanceolate, 30-70 × 8-36 mm, herbaceous; bases attenuate to cuneate, clasping, more so distally; margins of distal half of blades coarsely dentate to serrate, apices acute to attenuate; midvein prominent, 1-2 pairs of smaller, ± parallel collateral veins often evident, both surfaces densely stipitate glandular, also often bearing resinous globules. Capitulescences usually monocephalous or with up to 5 capitula in an elongate or flat-topped cyme. Capitula discoid. Involucres campanulate to hemispheric, 10-12 × 7-10 mm. Phyllaries 2-3 seriate, 21-28, subequal, imbricate, outermost leaflike, broadly ovate, 3-nerved, stipitate glandular, slightly spreading, apices obtuse with small mucro, inner bracts narrower, lanceolate-spatulate, margins finely ciliate, apices acuminate-cuspidate. Receptacles convex, alveolate. Ray florets 0. Disk florets (29-)35-50(55), bisexual, corollas golden-yellow, (5.8-)6.4-7.1(-7.6) mm, lobes (1-)1.3(-1.6) mm, lanceolate, slightly spreading to recurved. Anthers yellow, about 2.6 mm. Style branches 1.8-2.5 mm, appendages narrowly lanceolate, 1.2-1.7 mm.

Cypselae cylindrical to fusiform, 4–5 mm, pubescent. Pappi tannish, ca. 25 setose bristles, 6–7 mm.  $x = 9$ .

*Etymology*.—Named for the Toiyabe Mountain Range, Nevada. Toiyabe is said to be a Shoshone Indian word meaning “Black Mountains.”

*Prominent features, distribution, and relationships*.—*Toiyabea* is monotypic and is known from the Toiyabe and Toquima mountains of southern Nevada. This species was originally described as *Haplopappus* (Anderson 1980) and later transferred to *Tonestus* (Nesom & Morgan 1990). Analyses based on DNA sequence data fail to support the monophyly of *Tonestus* sensu Nesom & Morgan (Roberts 2002; Roberts & Urbatsch 2004; Brouillet et al. 2004). Close affinity of *Toiyabea alpina* to *Tonestus eximius* (H.M. Hall) A. Nelson & Macbride and to *Tonestus peirsonii* (Keck) Nesom & Morgan suggested by morphological similarity is likewise not supported by sequence data (Roberts & Urbatsch 2004). Evolutionary affinities of *Toiyabea* appear to be with *Petradoria* and the clade composed of *Stenotus acaulis* and *S. armerioides* (Fig. 1).

***Toiyabea alpina*** (L.C. Anderson & S. Goodrich) R.P. Roberts, Urbatsch & Neubig, comb. nov. *BASIONYM*: *Haplopappus alpinus* L.C. Anderson & S. Goodrich, *Great Basin Naturalist* 40:73. 1980. *Tonestus alpinus* (L.C. Anderson & S. Goodrich) G.L. Nesom & D.R. Morgan, *Phytologia* 68:177. 1990. TYPE: UNITED STATES, NEVADA. [Nye Co.] granitic rocks at 10,600 ft on 11,077 ft peak on Toiyabe Crest between Washington Creek and Aiken Creek, 2.4 air mi SSW of Austin, 1979, L.C. Anderson 4885 (HOLOTYPE: BRY).

*Distribution, ecology, and relationships*.—*Toiyabea alpina* inhabits rocky terrain near and above the tree line on the Toiyabe and Toquima mountains of southern Lander and Nye counties, Nevada (Anderson 1980). This taxon occurs infrequently on various substrates and might be of conservation concern. It is found in association with several other species of Asteraceae and other alpine endemics of Nevada, including *Draba arida* C.L. Hitchc. and *Geranium toquimense* N.H. Holmgren & A.H. Holmgren (Anderson 1980). Plants of this species flower from mid-summer into the fall. In his description of the species, Anderson (1980) highlighted vegetative and reproductive features that suggested a close relationship with *Tonestus* (*Haplopappus*) *aberrans* (A. Nelson) G.L. Nesom & D.R. Morgan and *T. (Haplopappus) eximius* A. Nelson & J.F. Macbr. The sequence-based investigations did not confirm these relationships. Instead, *Tonestus aberrans* was assessed to be more closely aligned with the *Machaerantherinae*, resulting in the description of the genus *Triniteurybia* to accommodate that taxon (Brouillet et al. 2004). In addition, the position of *Tonestus eximius* was either not fully resolved or else weakly aligned in a grade below *Chrysothamnus* sensu Urbatsch et al. (2005). *Toiyabea alpina*, for the most part, received moderate to strong support in a clade in which it was unresolved with *Petradoria pumila* and *Stenotus acaulis*/*S. armerioides* (Roberts 2002; Roberts & Urbatsch 2004). *Toiyabea alpina* can be distinguished from the two species of *Stenotus* by its similar basal and cauline leaves, leaf-like outer phyllaries,

and discoid capitula. Its closest evolutionary affinities appear to be with *Petradoria*, from which it is distinguished by its densely stipitate-glandular pubescent, spatulate, ovate or oblanceolate leaves with coarsely toothed margins, foliaceous phyllaries, and eradiate capitula producing 35 or more bisexual disc florets.

#### KEY TO *NESTOTUS*, *PETRADORIA*, *STENOTUS*, *TOIYABEA*, AND RELATED TAXA

1. Capitula in a densely corymbiform capitulescence, 5 or more per cluster; involucre cylindrical to turbinate, up to 3 mm broad, phyllaries strongly graduated; disk flowers 2–4 per capitulum, functionally staminate, ray flowers 1–3 \_\_\_\_\_ **Petradoria**
1. Capitula solitary or capitulescence at most with 4 per cluster, scape; involucre campanulate to hemispheric, more than 3 mm broad, phyllaries subequal to graduated; disk flowers 12+ per capitulum, bisexual, ray flowers 0 or 5–17.
  2. Leaf margins coarsely toothed, cauline (peduncular) leaves well-developed and similar to basal leaves; phyllaries wholly foliaceous; Lander and Nye counties, Nevada \_\_\_\_\_ **Toiyabea**
  2. Leaf margins entire, cauline (peduncular) leaves much reduced or absent; phyllaries chartaceous at least proximally; not known from Lander and Nye counties (except for *S. acaulis*).
  3. Capitula discoid; Sierra de San Pedro Mártir, Baja California \_\_\_\_\_ **Stenotus pulvinatus**
  3. Capitula radiate; western U.S.A. and Canada.
    4. Shoots villous to lanate with long, crinkly hairs and stipitate, glandular trichomes; taproots poorly developed \_\_\_\_\_ **Stenotus lanuginosus**
    4. Shoots with short, straight or arching conic hairs, glandular hairs sometimes also present; taproots usually well-developed,
      5. Phyllaries weakly imbricate, phyllary apices acute, green portion much longer than broad often extending full length of phyllaries; leaves generally bearing short, gland-tipped hairs; intergrades with *S. armerioides* occur in Colorado and eastern Wyoming \_\_\_\_\_ **Stenotus acaulis**
      5. Phyllaries regularly imbricate, phyllary apices obtuse to rounded, green portion about as long as broad and generally restricted to the distal one-third; leaves viscid or viscid dotted, stalked hairs not evident \_\_\_\_\_ **Stenotus armerioides**

#### KEY TO SPECIES OF *NESTOTUS*

1. Leaf surfaces glabrous, margins often ciliate; Yukon River drainage, Yukon Territory, Canada \_\_\_\_\_ **N. macleanii**
1. Leaf surfaces and margins abundantly pubescent with gland-tipped trichomes; northwestern U.S.A. \_\_\_\_\_ **N. stenophyllus**

#### ACKNOWLEDGMENTS

The authors thank the curators and staff personnel of ASC, ASU, BRY, CAS, DH, RM, UNLV, US, UT, and WTU for specimen loans on which this and related research is based. We thank Mario Blanco and Lorena Endara for preparing the Spanish abstract and Guy Nesom and others for their helpful comments.



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